

<i>Bollettino della Società Paleontologica Italiana</i>	33 (1), 1994	ISSN 0375-7633	51-70	3 pls.	Modena, Maggio 1994
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New observations on the Lower Cretaceous fish *Notagodus pentlandi* Agassiz (Actinopterygii, Halecostomi, Macrosemiidae)

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KEY WORDS – Fishes, Systematics, New taxon (Neonotagodus), Cretaceous (Barremian-Albian), Southern Italy.

ABSTRACT – A more comprehensive description of *Notagodus pentlandi* Agassiz, the type species of the genus, is given on the basis of the specimens in the collections of the Museum of Palaeontology of Naples and of the Natural History Museum in London.

Four new well preserved specimens from the «Calcari ad Ittioliti» of Pietraroia (Southern Italy) are described. Newly described features are the mandibular sensory canal which is found to be completely enclosed by bone, the completely ossified coracoid. These features are unusual in macrosemiids and differentiate *N. pentlandi* from all the other members of the genus. An account about the structure of the caudal skeleton (poorly known in Macrosemiids) is also given.

Differences between *N. pentlandi* and *N. denticulatus* Agassiz are confirmed and based on the above mentioned features. *N. denticulatus* is proposed as the type species of a new genus *Neonotagodus*, grouping more derived species.

RIASSUNTO – [Nuove osservazioni su *Notagodus pentlandi* Agassiz (Pisces, Actinopterygii, Halecostomi, Macrosemiidae)] – Viene fornita una più completa descrizione di *Notagodus pentlandi* Agassiz, specie tipo del genere, sulla base degli esemplari già presenti nelle collezioni del Museo di Paleontologia dell'Università di Napoli e del British Museum (Natural History) di Londra e di alcuni nuovi esemplari derivanti da uno scavo paleontologico condotto presso Pietraroia (BN). Le osservazioni condotte hanno consentito di differenziare con certezza *N. pentlandi* da *Notagodus denticulatus* Agassiz, evidenziando inoltre, nella prima specie, l'esistenza di caratteri mai osservati prima nei rappresentanti del genere *Notagodus* e, più in generale, nelle forme ascritte alla famiglia Macrosemiidae. Tali caratteri (canale sensoriale mandibolare completamente incluso nell'osso ed apertesi all'esterno attraverso pori; completa ossificazione del processo anteriore del coracoide) avvicinano maggiormente *N. pentlandi* alla condizione di Macrosemiide primitivo ed inducono ad uno smembramento del genere, viene pertanto proposta l'istituzione del nuovo genere *Neonotagodus*, raggruppante le forme con caratteri meno primitivi, la cui specie tipo sarà *Notagodus denticulatus* Agassiz.

INTRODUCTION

In September-October 1982, the Department of Paleontology of the University of Naples, in collaboration with the Museo Civico di Scienze Naturali in Turin, ran an excavation in the famous Lower Cretaceous fossiliferous beds known as «Calcari ad ittioliti di Pietraroia» (Costa, 1851-1866; Bassani, 1882, 1892; D'Erasmus, 1911, 1915; D'Argenio, 1963a, b, c; Catenacci & Manfredini, 1963; Freels, 1975; Bravi, 1988a and b), outcropping in Civita di Pietraroia (I.G.M. sheet 162 - III SW - Cusano Mutri).

Excavations were conducted in a locality named «Le Cavere», where the fossiliferous beds are best exposed and richest in fossils.

During the excavation more than 250 specimens, mainly fishes, were collected. The discovery of four well preserved specimens of *Notagodus pentlandi* Agassiz led me to restudy this species because of our incomplete knowledge of its osteology and of the

controversial opinions about its relationships to other species of the same genus.

N. pentlandi was established by Agassiz (1835) on the basis of specimens from Castellammare di Stabia (Naples); the species was subsequently studied by Woodward (1895b), Bassani & D'Erasmus (1912) and D'Erasmus (1915), using poorly preserved specimens from Castellammare and Pietraroia.

Bartram (1977), in a revision of the Family Macrosemiidae, reported that the available specimens of *N. pentlandi* «reveal little detail, since the bones are largely shattered beyond recognition». Bartram (op. cit., p. 202) thought it possible that the species is not distinct from *N. denticulatus* Agassiz.

The new specimens, observation of the type specimen at the N.H.M., London, and of other specimens from Pietraroia and Castellammare at the Museum of Palaeontology in Naples, together with observation of specimens of *N. denticulatus* at the N.H.M. allow me to give a more comprehensive description and illustration of the osteology of *N.*

pentlandi. They also allow a reassessment of the relationships of this species to the better known *N. helenae* and *N. denticulatus* as well as allowing *N. pentlandi* to be clearly distinguished from *N. denticulatus*.

GEOLOGIC SETTING

a) PIETRAROJA

«Civita di Pietraroja» (Text-fig. 1) is a monocline structure reaching 960 m above sea level, situated near the eastern edge of the Matese massif. The structure is bounded by very steep fault slopes on all but the East side: the dray slope constitutes the plateau of the Civita.

The body and the edges of the monocline are dissected by NW-SE and NE-SW trending faults, forming high subvertical slopes. In the deep valleys around the Civita flow the Tiberino river and Rio Torbido. The average dip of the strata is 15 E-SE.

The outcropping sequence is constituted by Lower Cretaceous limestones and dolomitic limestones up to 300-320 m thick; it is possible to distinguish two main parts in the sequence (D'Argenio, 1963c):

- lower part: about 250 m of brown and grey fossiliferous intramicrites often with green clay and marl layers in the upper part, where bed thickness decreases. Limestones and dolomitic limestones are also present.

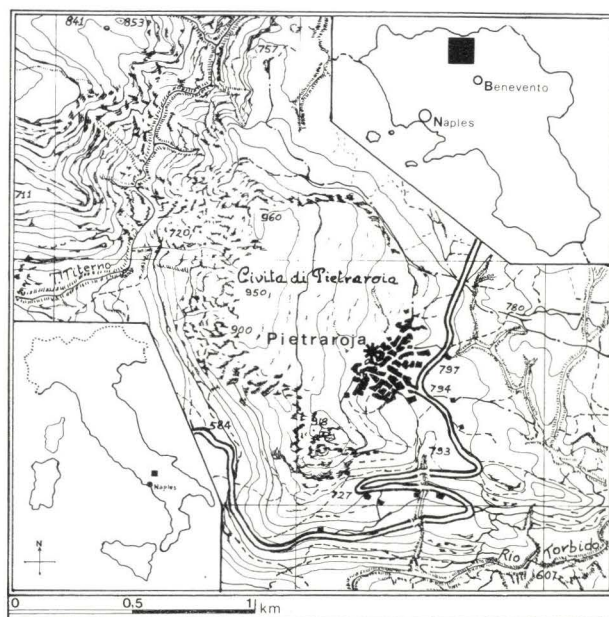
Toward the bottom of the lower portion there are traces of small rudists (*Requienia*?) and gastropods resembling *Nerinea*.

Towards the top there are only remains of indeterminate bivalves and gastropods.

- upper part: 50-70 m of fossiliferous micrites, intramicrites and intrasparrudites. Basally, this part is made up of thin beds with fragmentary indeterminate molluscs. This gradually passes up into detrital white, tawny and brown limestones, sometimes oolitic or pseudoolitic, with remains of small rudists, turreted gastropods and oysters. Microfossils are *Cuneolina camposauri* Sartoni & Crescenti, *C. laurentii* Sartoni & Crescenti and *Salpingoporella dinarica* Radoicic, locally associated with *Orbitolina* spp. and charophytes (Catenacci & Manfredini, 1963).

The «Calcari ad ittioliti di Pietraroja» constitutes a heteropic facies locally present in the upper part of the sequence. They contain thin detrital levels with *Cuneolina* spp., Miliolidae, Textulariidae, *Glomospira*, Orbitolinidae, and Ostracods.

According to Catenacci & Manfredini (1963) this microfauna is the same of that contained in the last



Text-fig. 1 - Sketch map of «Civita di Pietraroja». (I.G.M. map 1/25.000, 162 III SW - Cusano Mutri).

strata of the Mesozoic sequence of the «Civita di Pietraroja».

On the grounds of this microfauna and other microfaunas in the southern Appennines (De Castro, 1962; Sartoni & Crescenti, 1962; Catenacci, De Castro & Sgroso, 1963), Catenacci & Manfredini ascribe the entire sequence to the Lower Cretaceous, except for the lowermost beds which are probably late Jurassic.

In particular, the portion that includes the «Calcari ad ittioliti» was dated Barremian-Albian, and most probably Aptian, because of the presence of *Salpingoporella dinarica*.

Current researches by S. Bravi and P. De Castro show that the «Calcari ad ittioliti di Pietraroja» must be attributed to the Lower Albian on the ground of the Orbitolinids and other microfossils as *Ovalveolina reicheli* De Castro found in the beds immediately below.

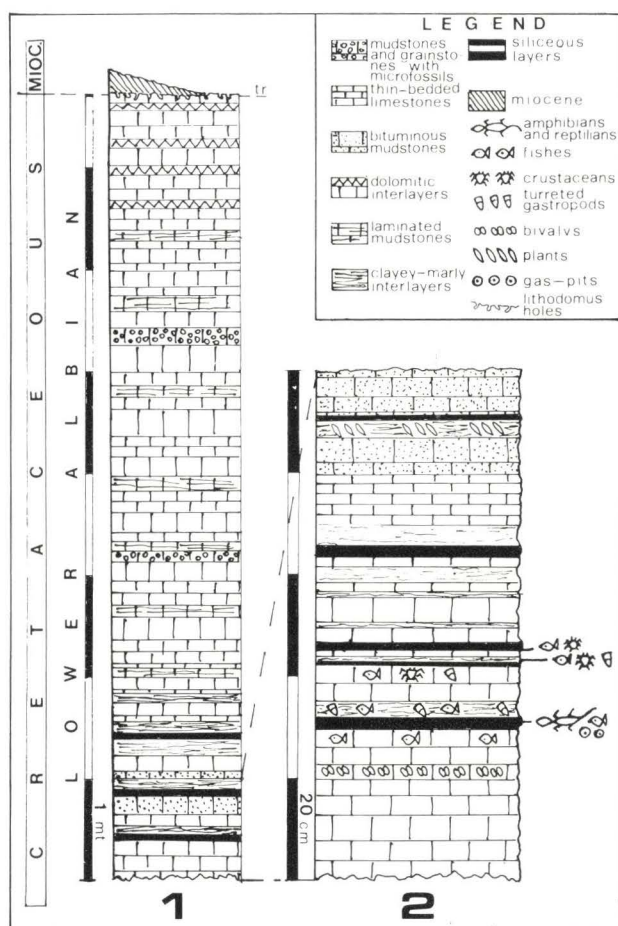
The Mesozoic sequence is unconformably overlain by Miocene limestones, partially of biostromal origin. This neritic Miocene sequence passes up into marls with *Orbulina* of the «Longano Formation». At the top of the sequence are flysch sediments, mainly turbidites, («Pietraroja Formation»), outcropping in the southern side of the «Civita».

The «Calcari ad Ittioliti» were interpreted by D'Argenio (1963c) as a shallow water, lagoonal sediment, deposited in an environment often subject

to drying out (evidence of this are mud cracks, gas-pits and edgewise breccias). D'Argenio attributed the frequent mass-mortalities, witnessed by the ichthyolitic beds, to the anoxic environment caused by interruption of water exchange with the open sea, and to the death of phytoplankton. More or less different interpretations are given by Catenacci & Manfredini (1963) and Freels (1975).

Recent observations (Bravi, 1987) confirm the shallowness of the water in the basin and its frequent retreat; it is also possible that rivers draining the nearby land were intermittently in communication with the basin.

The «Calcari ad Ittioliti» (Text-fig. 2) also yield reptiles, amphibians and plant remains, including probable *Cycadales*.



Text-fig. 2 - Stratigraphical column of «Calcari ad ittioliti» at «Le Cavere». 1) Simplified stratigraphical column, from the first stratus outcropping in the bottom of the quarry to the Miocene transgression on the top of the cretaceous sequence. 2) Sketch of the first meter of the sequence. This is the more rich in fossils part in the sequence.

b) CASTELLAMMARE

The ichthyolitic beds of Castellammare (I.G.M. sheet 1:25.000 184 II SE - Punta Orlando) outcrop between the Km 12 and Km 14 of the coastal state road N. 145, between Castellammare di Stabia and Vico Equense. They do not exceed 10 m, and they are included in the lower part of a calcareous series, outcropping from sea level to the top of Mt. Pezzulli (452 m), constituted by a cyclic sequence of dark mudstones, wackestones and grainstones alternating with dolomitic beds and belonging to an inner platform lagoon depositional environment.

Historical accounts on the fish deposit were supplied mainly by Breislak (1798), Alvino (1842) and, more recently, by Leuci (1976).

The age of the ichthyolitic level or, more generally, of the entire sequence, was discussed mainly by Agassiz (1833-43, vol. II, 2, p. 190: Jurassic), Guiscardi (1866) and Bassani (1890) (Neocomian), Bassani & D'Erasmo (1912, Cenomanian, together with the «Calcari ad ittioliti» of Pietraroia). Because of the presence of a distinctive guide-level - «Livello ad Orbitoline» - that lies some tens of meters above the ichthyolitic beds, some of the datings of the sequence were made on the basis of the micro and macrofossils included in this level and then extended to the fishes deposit. On this basis De Castro (1962), De Castro, Cherchi & Schroeder, (1978) gave an age bracketed between Barremian and Albian (probably Aptian) to the sequence comprising the ichthyolitic beds and the «Livello ad Orbitoline».

Current researches by S. Bravi and P. De Castro have stressed the presence of an association with *Salpingoporella melitae* (Radoicic), *S. muehlbergii* (Lorenz), *Praturlonella danilovae* (Radoicic) and *Campanellula capuensis* De Castro in the beds immediately below the ichthyolitic level. Since the «Livello and Orbitoline», which is characteristic of the Upper Aptian (Middle Gargasian), lies 70-80 m above, and taking into account the new data, the ichthyolitic limestones of Castellammare must be dated Lower Barremian.

DESCRIPTION

Infraclass NEOPTERYGII
Division HALECOSTOMI
Subdivision *incertae sedis*
Family MACROSEMIIDAE

Genus NOTAGOGUS Agassiz, 1835 [emend.]
NOTAGOGUS PENTLANDI Agassiz, 1835 [emend.]

1835 *Notagodus pentlandi* AGASSIZ, p. 10 and 294, pl. 49, fig. 2.
1835 *Notagodus latior* AGASSIZ, *ibidem*, fig. 3.

- 1853 *Notagodus pentlandi* Agassiz - COSTA, p. 312, pl. 5, fig. 2; pl. 7, fig. 5.
 1853 *Notagodus erythroplepis* Costa - COSTA, p. 314, pl. 4, figs. 6-7.
 1853 *Notagodus minor* Costa - COSTA, p. 315, pl. 5, fig. 4.
 1853 *Blenniomoerus longicauda* Costa - COSTA, p. 319, pl. 6, fig. 2.
 1853 *Blenniomoerus brevicauda* Costa - COSTA, p. 321, pl. 5, fig. 3.
 1856 *Blenniomoerus maior* Costa - COSTA, p. 34, pl. 2, figs. 4-6.
 1856 *Calignathus* sp. Costa - COSTA, p. 37, pl. 4, fig. 6.
 1856 *Pachyodon* sp. Costa - COSTA, p. 38, pl. 4, fig. 7.
 1860 *Lepidotus exiguus* Costa - COSTA, p. 8, pl. 3, fig. 2.
 1864 *Lepidotus exiguus* Costa - COSTA, p. 75, pl. 11, fig. 2.
 1864 *Notagodus pentlandi* Agassiz - COSTA, p. 72, pl. 12, fig. 5.
 1864 *Notagodus crassicauda* Costa - COSTA, p. 74, pl. 12, figs. 6-7.
 1864 *Blenniomoerus longicauda* Costa - COSTA, p. 99, pl. 11, figs. 9-10.
 1864 *Notagodus erythroplepis* Costa - COSTA, p. 102, pl. 11, fig. 11.
 1864 *Notagodus gracilis* Costa - COSTA, p. 103, pl. 11, fig. 8.
 1864 *Notagodus crassicauda* Costa - COSTA, p. 91, pl. 7, fig. 1 (a, b, c).
 1882 *Notagodus pentlandi* Agassiz - BASSANI, pp. 237-239.
 1895b *Notagodus pentlandi* Agassiz - WOODWARD, p. 186, pl. 3, fig. 7-8.
 1911 *Notagodus pentlandi* Agassiz - D'ERASMO, pp. 798-799.
 1912 *Notagodus pentlandi* Agassiz - BASSANI & D'ERASMO, p. 206, pl. 3, figs. 1-2; pl. 4, figs. 1-2; pl. 5, fig. 1.
 1915 *Notagodus pentlandi* Agassiz - D'ERASMO, p. 47, pl. 6, figs. 1-4.
 1977 *Notagodus pentlandi* Agassiz - BARTRAM, pp. 201-202.

Holotype - The Natural History Museum, London; specimen 117.

Topotypes - P2065, P6866, P1097a, b, c. N.H.M., London; M291, M635, M636, M637, M638, M639, M640, M641, M642, M643, M644, M645, M646, M647, M648, M672, M675. M.P.N., Naples.

Type locality - Capo d'Orlando, Castellammare di Stabia (NA).

Type horizon - Calcare ad ittioliti di Capo d'Orlando. Age: Barremian.

Other material - M292, M294, M295, M296, M297, M299, M300, M301, M302, M303, M304, M492, M500, M509, M517, M518, M519, M19270, M19271, M19277, M19297 from «Calcari ad Ittioliti di Pietraroia» (Southern Italy), Lower Albian. M.P.N., Naples.

Material - All the above mentioned specimens of

N. pentlandi from Castellammare (Capo d'Orlando), at present deposited in The Natural History Museum, London (N.H.M.) and in the Museum of Paleontology of Naples (M.P.N.), have been examined; this material is poorly preserved on the whole. Other material is constituted by the specimens of *Notagodus* from Pietraroia, assigned to the species *pentlandi* by Bassani & D'Erasmus (1912) and D'Erasmus (1915). Some of this material is better preserved than that from the type locality. Four new specimens from Pietraroia (M19270, M19271, M19277, M19297) discovered during the excavation campaign carried out during the year 1982, are the best preserved.

Therefore much of the following description is based on these specimens that show some features never observed in the species.

At The Natural History Museum, London, I was also able to examine some specimens of *Notagodus denticulatus* (P1089, P1090, P3610, P3611), which is doubtfully differentiated from *N. pentlandi* (see Bartram 1977, p. 202). Throughout the description, will often be made reference to *N. helenae* and *N. denticulatus* in describing some bones because these two species are the better known following the revision by Bartram (1977).

COMPARISON BETWEEN THE SPECIMENS FROM CASTELLAMMARE AND PIETRAROIA

The examination of the holotype and topotypes of *N. pentlandi* in the collection of N.H.M. and of the topotypes in the collection of the Museum of Paleontology of Naples has reconfirmed that all the specimens from Castellammare (Capo d'Orlando) belong to the same species.

The specimens of *Notagodus* from Pietraroia were studied by D'Erasmus (1915) and ascribed to *N. pentlandi* by this Author for their «complete and perfect correspondence with the specimens from Castellammare» (op. cit., p. 75). Actually the specimens from Castellammare are poorly preserved on the whole, so it is impossible to perfectly compare of all their parts with the well preserved specimens from Pietraroia; however it has been

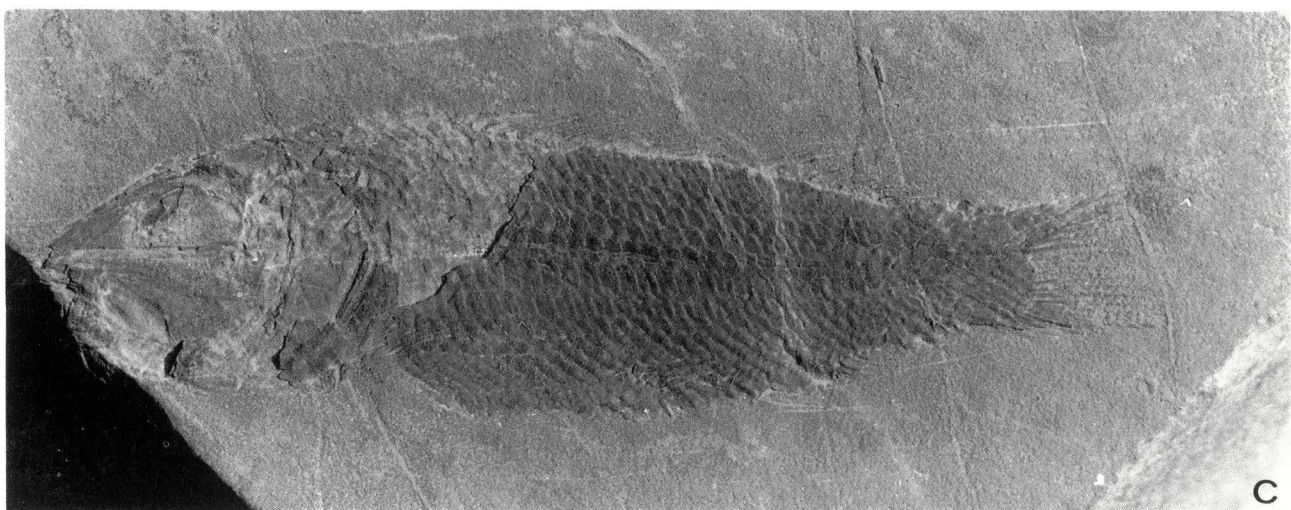
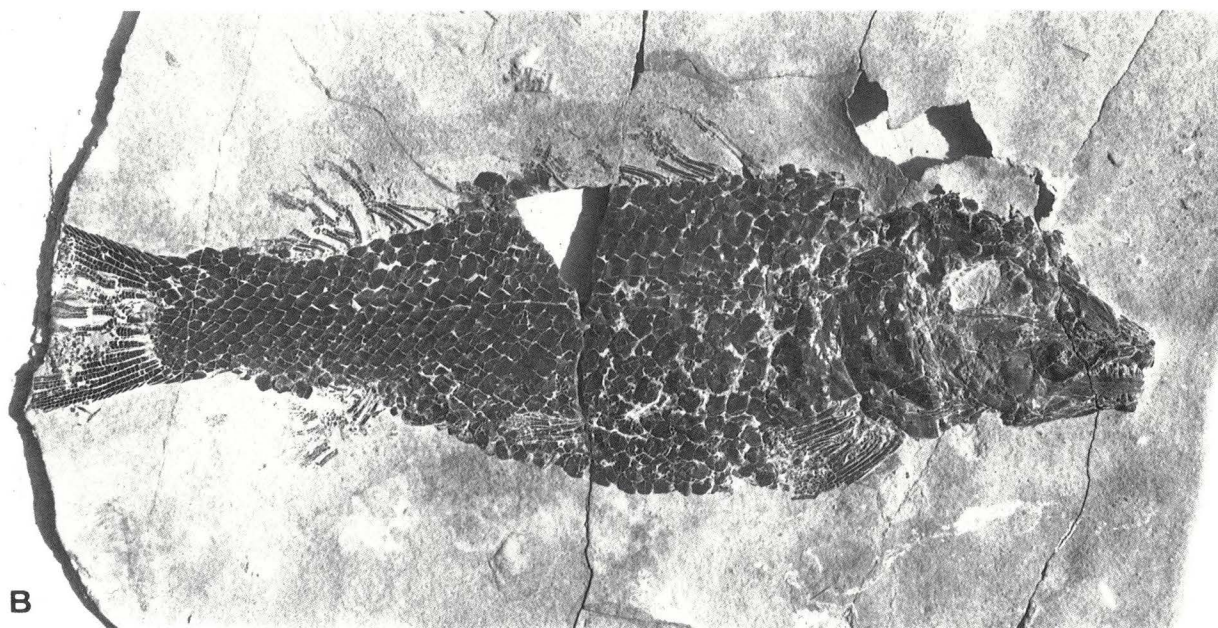
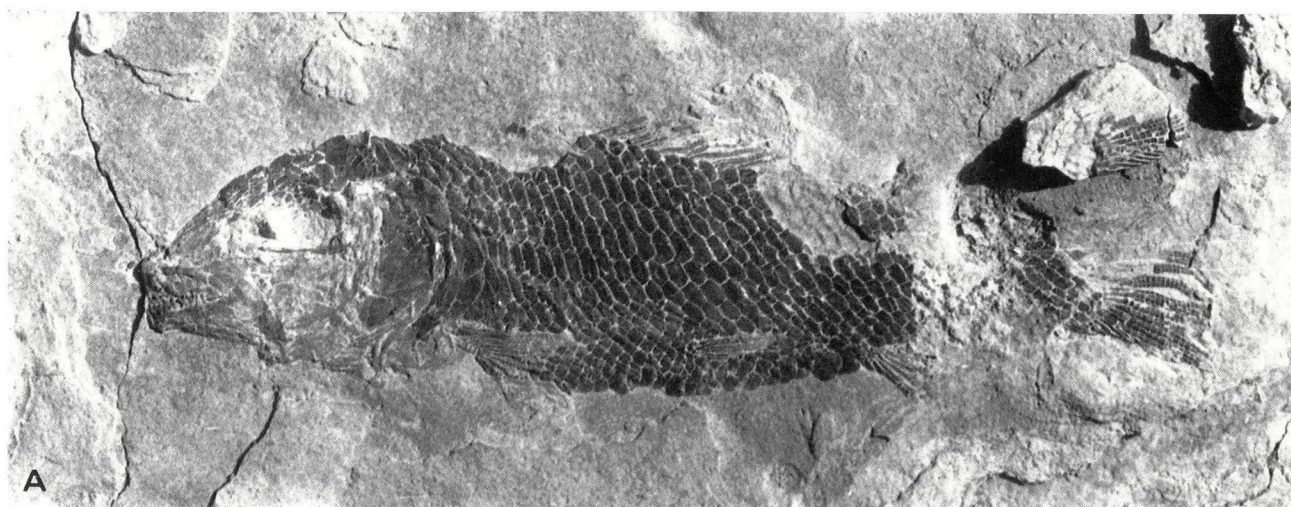
EXPLANATION OF PLATE 1

Notagodus pentlandi Agassiz.

Fig. A - Specimen M19271, «Calcari ad ittioliti». Lower Albian of Pietraroia, Southern Italy. X 1.3 approx.

Fig. B - Specimen M19277, «Calcari ad ittioliti». Lower Albian of Pietraroia, Southern Italy. X 1.0 approx.

Fig. C - Specimen M648. Lower Barremian of Castellammare di Stabia, Southern Italy. X 2.3 approx.



possible to confirm at least the identity of the following features:

- 1) the arrangement and number of the rays in the fins;
- 2) the presence of rows of polygonal supraorbitals;
- 3) the number of the lateral line scales;
- 4) the pattern of squamation;
- 5) the shape of the preanal scale;
- 6) the shape of some dermal bones in the head [e.g.: the maxillar in BM(NH) 117].

Biometric measures are also similar, expressed as percentages of standard length, the only exception seems to be the mean prepelvic length (Ppl) that is 58% in the specimens from Castellammare, and 62% in the specimens from Pietraroia, but this measure is doubtful in some poorly preserved specimens.

To better evaluate this possible difference between the two populations, which are incidentally separated in time (see above), regression lines have been calculated using the main biometric measures of the specimens (Table 3) belonging to the two populations (some examples are shown in text-figs. 3, 4). Every pair of regression lines shows a good agreement between them. However, the resulting differences have been tested by carrying out a statistic analysis on the biometric measures using the test of covariance (Lison, 1982). The following values have been obtained:

SL-HL	:	F = 1.7682	(-)
SL-PdL	:	F = 2.0750	(-)
SL-BD	:	F = 0.0371	(-)
SL-PpL	:	F = 9.2857	(++)
SL-PaL	:	F = 1.5868	(-)
PpL-HL	:	F = 0.3172	(-)
PpL-BD	:	F = 2.0252	(-)
PpL-PdL	:	F = 1.0568	(-)
PaL-HL	:	F = 0.2111	(-)
PaL-BD	:	F = 0.3620	(-)
PaL-PdL	:	F = 0.5684	(-)
PaL-PpL	:	F = 8.0140	(+)
PdL-HL	:	F = 0.0000	(-)
PdL-BD	:	F = 2.4394	(-)
HL-BD	:	F = 2.3951	(-)

Tab. 1 - Results of the covariance test on the specimens of *Notagodus* from Castellammare and Pietraroia. (-) = not significant; (+) = significant; (++) = highly significant.

The test has not supplied significant values of F for any of the compared parameters except for SL-PpL and PaL-PpL. These do vary significantly different between the two populations, but it is probably due to poor preservation mentioned above. Thus, the test of covariance has confirmed the statistic homogeneity between individuals from the two populations (Castellammare and Pietraroia).

The same test has been applied to compare some biometric measures of six specimens of *N. helenae* (see Saint-Seine, 1949; p. 194), with those of the specimens from Castellammare and Pietraroia. The results of the tests are the following:

N. helenae - *N. Castellammare*

SL-HL	:	F = 0.4466	(-)
SL-BD	:	F = 9.3191	(++)
BD-HL	:	F = 10.819	(++)

N. helenae - *N. Pietraroia*

SL-HL	:	F = 0.1193	(-)
SL-BD	:	F = 8.1843	(+)
BD-HL	:	F = 9.6994	(++)

Tab. 2 - Results of the covariance test between *N. helenae* and the *Notagodus* from Castellammare and Pietraroia.

The significant statistical differences between *N. helenae* and the *Notagodus* from Castellammare and Pietraroia constitute a further evidence to suggest the specimens from Castellammare and Pietraroia are conspecific.

Notagodus pentlandi Agassiz

Diagnosis (emended) - *Notagodus* reaching standard length of 130 mm; mean proportions as percentages of standard length: head length 33%, trunk depth about 29.50%, predorsal length 44%, preanal length 79%. Two rows of polygonal supraorbitals; mandibular sensory canal running in a tube, opening by 5-6 pores. Coracoid completely ossified. Two lobes of dorsal fin closely spaced.

Fin ray counts: D1 = 14-15, D2 = 10-12; P = at least 12 (15 ?); V = 6; A = 6-7; C = 13-14 (rarely 6/8, usually 5/8). 37-38 lateral line scales. Fringing fulcra

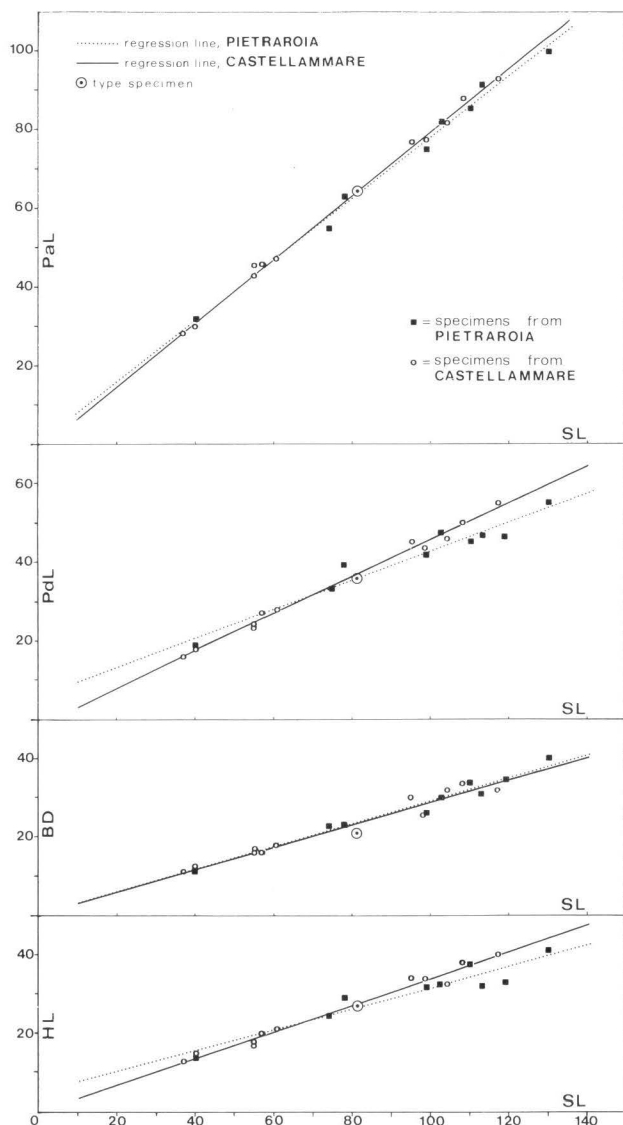
EXPLANATION OF PLATE 2

Notagodus pentlandi Agassiz. The head in

Fig. A - Specimen M19271. Lower Albian of Pietraroia. X 3.8 approx.

Fig. B - Specimen M19297. Lower Albian of Pietraroia. X 3.5 approx.





Text-fig. 3 - Regression lines of most significant parameters of *Notagodus pentlandi* Agassiz. Specimens are also indicated (circles and squares). Measurements are in millimetres. Abbreviations are explained in the Appendix.

are present on ventral, anal and caudal fins, the pectoral fins bear the remains of small fringing fulcra, fused with the leading ray. About 28 (30?) vertebral centra. Rhombic and hexagonal enamelled scales, with partially serrated hind margin; three post-cleithral scales; some ventral regions in the adults,

and all the body in young specimens, are covered by cycloid scales.

Measurements (in mm) -

Spec.	SL	BD	HL	PdL	PpL	PaL	Loc.
M635	98.5	25.5	34	43.5	60 ?	77.5	C
M637	60.5	18	21	28	36	47	C
M638	95	30	34	45	58	77	C
M639	37	11	12.5	16	23.5	28.5	C
M640	-	13	17	24	31	-	C
M643	-	27	29.5	41.5	-	71	C
M645	40	12.5	14.5	18	25	30	C
M646	108	33.5	38	50	68 ?	88	C
M647	55	17	17	24	34	43	C
M648	57	16	20	27	35	46	C
M672	55	16	17.5	23.5	38	45.5	C
M675	104	32	32.5	46	-	82	C
117 (TYPE)	81	21	27	36	-	64.5	C
P2065	117	32	40	55	-	93	C
M295	113	30.5	32	46.5	65	91.5	P
M301	78	23	29	39	48.5	63	P
M492	102.5	30	33	47.5	59.5	82	P
M517	40	12	14	18.5	24.5	32	P
M519	119	34.5	33	46.5	-	-	P
M19270	74	23	24.5	33	40	55	P
M19271	99	26	31.5	41.5	57.5	75	P
m19277	130	40	41	55	74	100	P
M19297	110	33.5	37.5	45	62	85.5	P

Tab. 3 - Measures in the better preserved specimens.

SL = Standard length; BD = Body depth; HL = Head length; PdL = Predorsal length; PpL = Prepelvic length; PaL = Preanal length; C = specimen from Castellammare; P = specimen from Pietrarroia.

SKULL ROOF AND BRAINCASE

(Text-figs. 5, 6, 7; Pl. 2, figs. A, B; Pl. 3, fig. A)

The arrangement and shape of the bones in the skull roof, is substantially similar to that of *N. bekenae* (see Bartram 1977, p. 197, fig. 41).

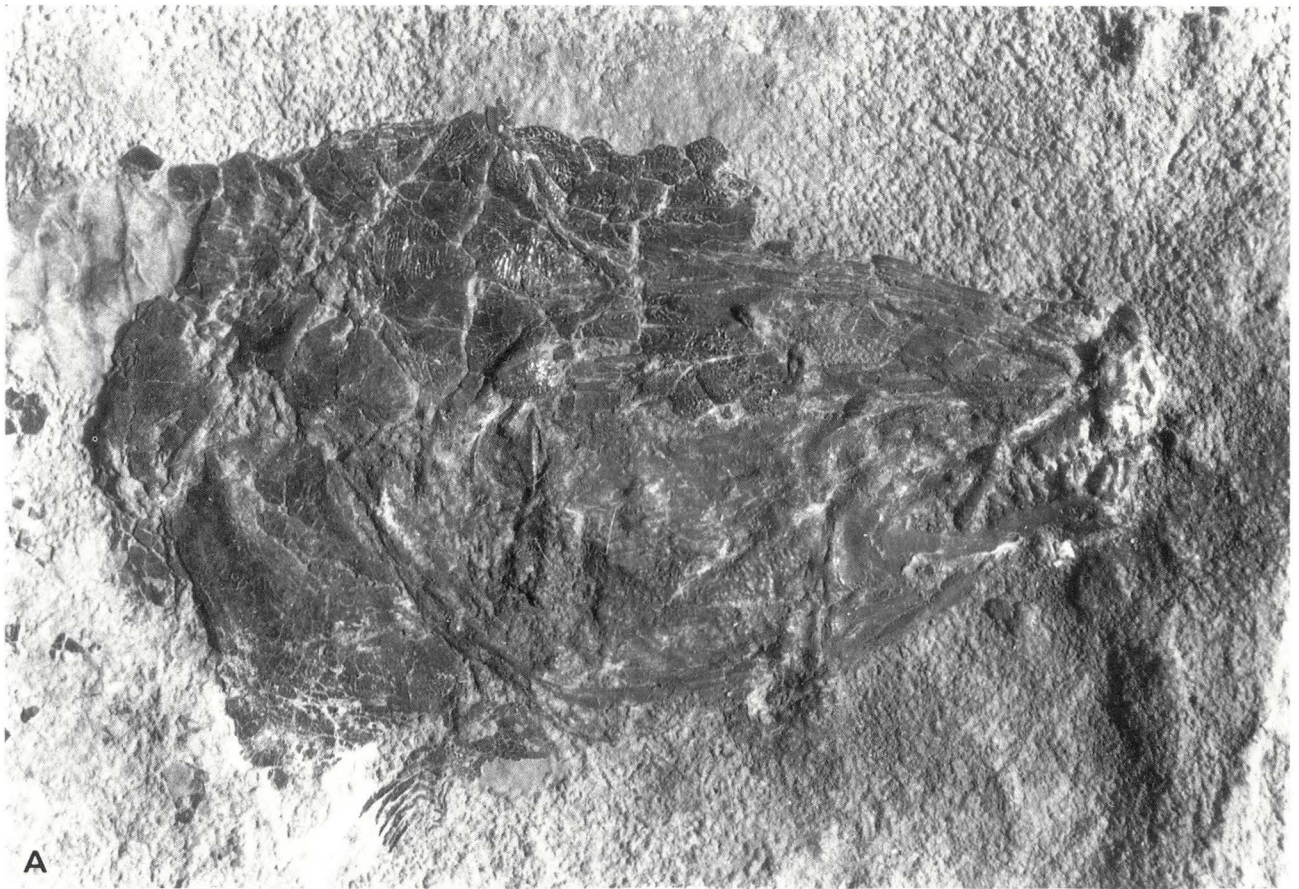
The frontals, slender and lacking ganoine in their anterior parts, quickly widen just before the orbit, forming an arched and pronounced orbital margin, bordered by ganoine tubercles and rugae, and with a few, small sensory pores. In the postorbital region the frontals form a slender finger between the

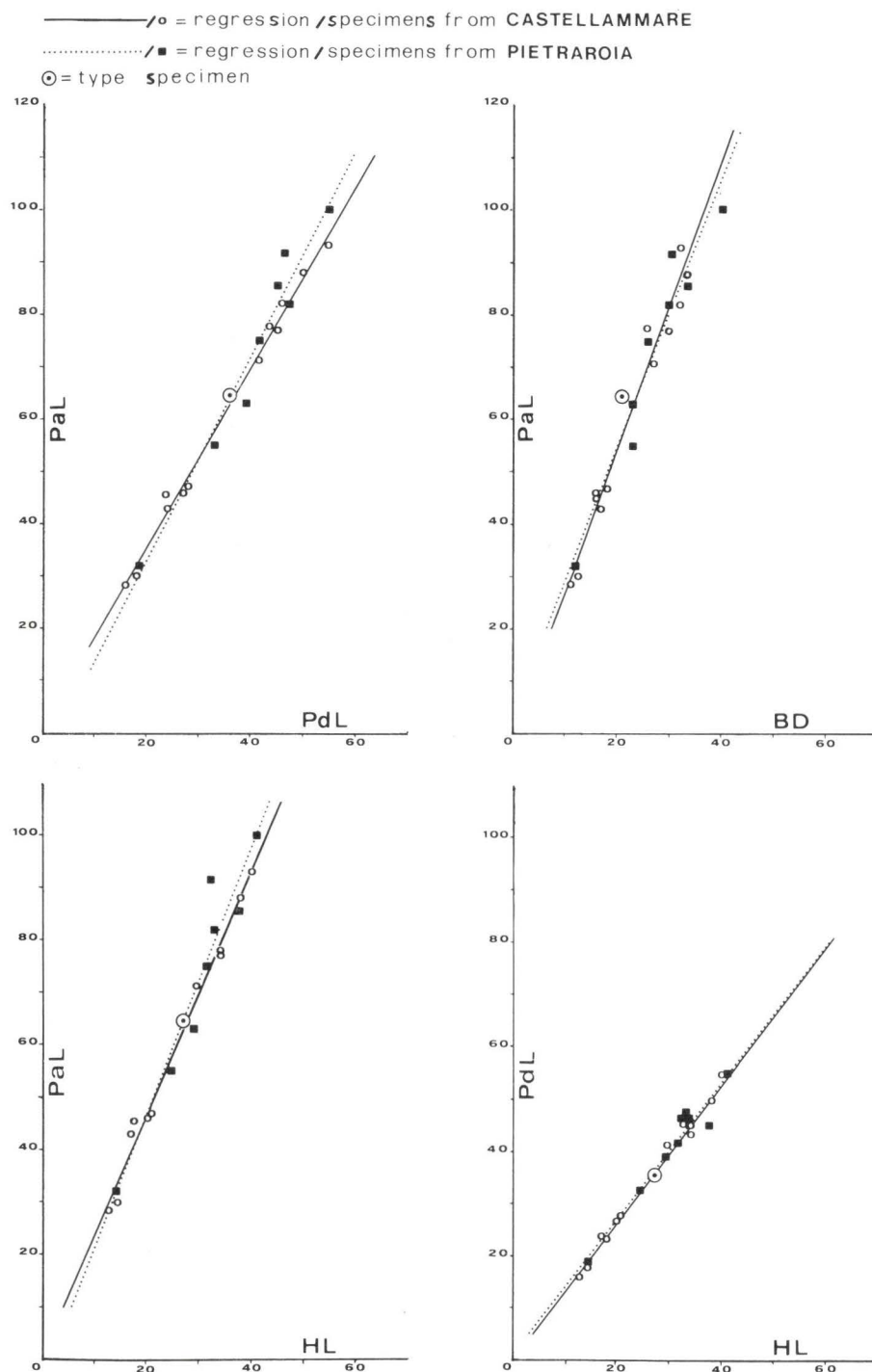
EXPLANATION OF PLATE 3

Notagodus pentlandi Agassiz.

Fig. A - Dorsio-ventrally fossilized skull-roof, specimen M500. Lower Albian of Pietrarroia. Two rows of supraorbitals are visible in the upper part of the photograph. X 4.3 approx.

Fig. B - Endoskeleton in specimen M647. Lower Barremian of Castellammare di Stabia. X 2.3 approx.

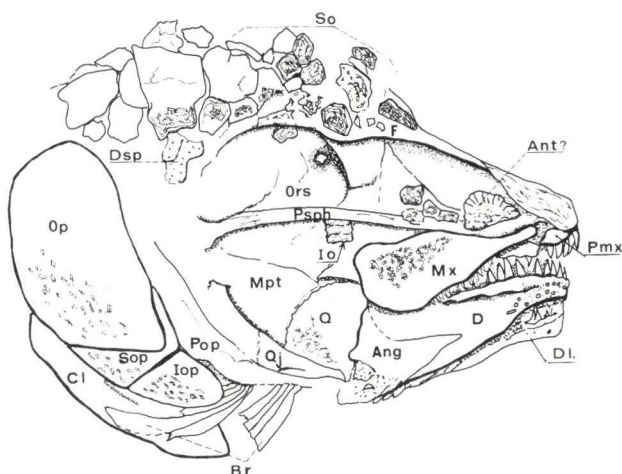




Text-fig. 4 - Regression lines of most significant parameters of *Notagogus pentlandi* Agassiz. Specimens are also indicated (circles and squares). Measurements are in millimetres. Abbreviations are explained in the Appendix.

supraorbitals and the parietals. The posterior and posteromedial borders of each frontal are slightly sinuous and transversally marked by ganoine rugae. In lateral view, the frontal narrows anteriorly, forming a deep ventral crest with a convex lower outline.

The parietals are broad and enamelled, with radiating ganoine ridges expressed near to the borders (Text-fig. 7). A posteromedial, semicircular suture lies on the right parietal in M19271 (Text-fig. 6), and the same condition is shown in M500 (Text-fig. 7), indicating a sinuous median suture along



Text-fig. 5 - *Notagodus pentlandi* Agassiz. Skull, as preserved in M19277.

which, the left or right parietal indifferently overlaps each other.

The dermosphenotic, relatively preserved in M19271, seems to resemble that of *Propterus elongatus*. In lateral view, it is a subtriangular and porous bony tube, opening by a large elliptical pore in the lower corner and with a flared dorsal end.

As usual in *Notagodus*, this bone encloses the union between the infraorbital and supraorbital sensory canals.

The dermopterotic is subtriangular and has a short and narrow groove ending with a pore near its dorsal corner. The pore marks the place where the supratemporal commissure enters the bone to run down and connect with the otic canal. The enamelled surface shows small ganoine tubercles only in the anterior corner.

The orbitosphenoid is thin and rather wide in the front of the orbit. Its posterior border is concave, the anterior one is convex.

The parasphenoid has a subtriangular cross section beneath the orbit, with a straight lower outline; it expands slightly posterior to the orbit, showing a lateral foramen for the efferent pseudobranchial artery. The posterior ascending process of the bone forms an angle of a little more than 90, at its base, with the horizontal portion.

CIRCUMORBITAL SERIES

In a previous brief paper (Bravi, 1988a) I described the frontal area covered by a mosaic of «polygonal frontal plates» in the *Notagodus* specimens from Pietraroia. Specimen M 500 in the collection of the Museum of Paleontology of Naples shows this interpretation to be incorrect. The «frontal plates» are two parallel rows of supraorbitals.

The more medial row of supraorbitals is in contact with the arched orbital margin of the frontal and the individual polygonal plates are bigger than those of the more lateral row; their surface is trimmed by ganoine tubercles and roughness. The total number of the supraorbitals is unknown, but in M500 eight plates are visible on the left side (Text-fig. 7) and in M19271 there are about ten plates, partly connected (Text-fig. 6).

The specimens from Castellammare, poorly preserved, show only few remains of supraorbitals, so it is possible to document only the upper row that, in M648, is exposed in medial view; the same specimen shows only few remains of probable supraorbitals belonging to the lower row.

In sum, the condition of the supraorbitals in the studied specimens is essentially similar to that described by De Saint-Seine (1949) for *N. helenae*.

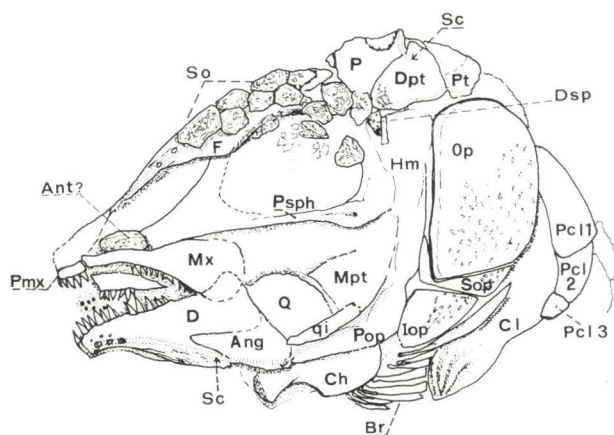
The specimens M19270, M19271 and M19277 show a rounded, thin plate, with a rough surface (Text-figs. 5, 6), in the same position of the «nasal» described by De Saint-Seine (op. cit., p. 195, fig. 85) for *N. helenae*; this plate can be probably considered an antorbital.

In M509, a row of seven infraorbitals is preserved. They are closely similar to those of *N. denticulatus*, forming delicate scrolls around the infraorbital sensory canal. Their complex number could be nine, as usual in Macrosemiids.

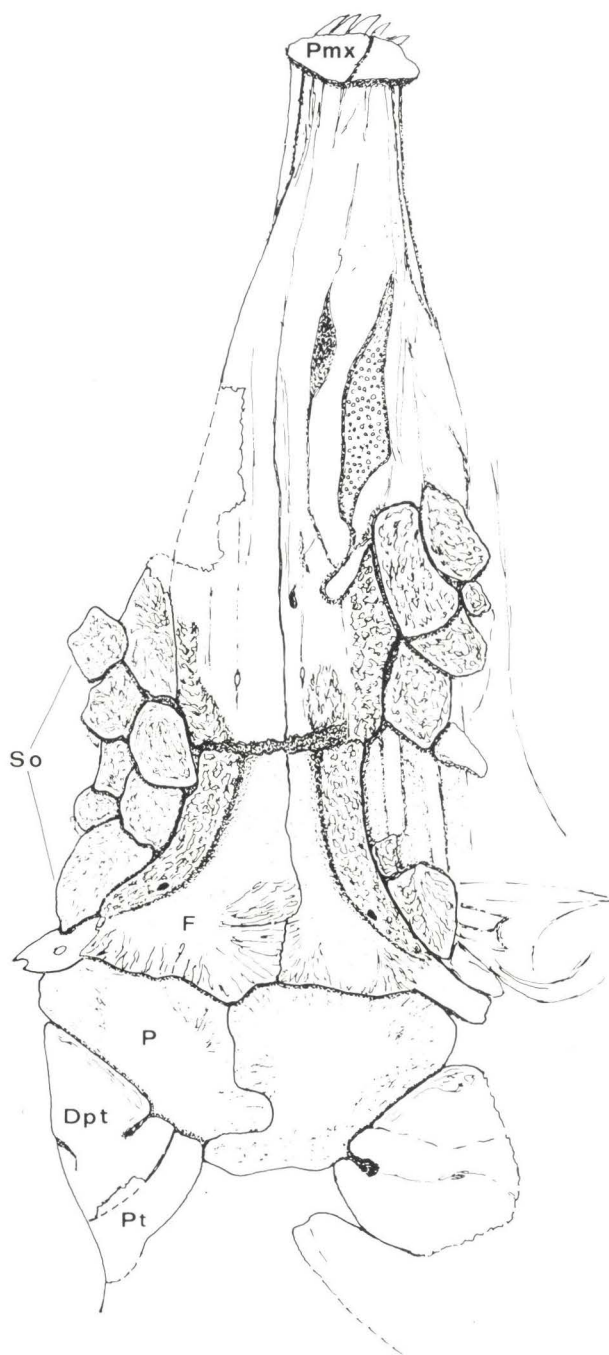
HYOPALATINE BONES

The quadrate is similar in shape to that of *N. denticulatus* (see Bartram 1977, pp. 192, 194, figs. 38-39). It has a rough surface and a convex and wavy posterior border.

The quadratojugal is similar to that of *N. inimon-*



Text-fig. 6 - *Notagodus pentlandi* Agassiz. Skull, as preserved in M19271.



Text-fig. 7 - *Notagodus pentlandi* Agassiz. Dorso-ventrally fossilized skull-roof, as preserved in M500.

tis (see Bartram 1977, p. 200, fig. 42), with an expanded posterior part.

The visible part of the metapterygoid is a bony leaf with a straight and horizontal upper border and a slightly concave lower edge. The lateral surface seems to be feebly corrugated.

The entopterygoid is only partially visible in all of the specimens. It is a broad, laminar bone, oc-

cupying all the area below the parasphenoid. The lower portion is hidden by the quadrate and metapterygoid.

DERMAL UPPER JAW

The premaxilla is a small, subtriangular thick bone. It bears four feebly curved, conical teeth of which the most anterior is the longest. The maxilla, as usual, has a cylindrical, anterior articular apophysis that fits with the ethmoid. The bone widens posteriorly to a rounded expansion.

The oral border, slightly concave, bears a long row of about 18 conical, pointed teeth; they are regularly spaced, smaller than the premaxillary teeth and they decrease in size posteriorly.

LOWER JAW

The dentary is rather oblong, with a square symphysis. Anteriorly it is low, with a slightly curved lower outline, whereas posteriorly it is considerably expanded. The dentary bears a row of at least ten conical teeth. The mandibular sensory canal runs in a tube that opens by four or five large sensory pores in the anterior half of the dentary. The collapsed lateral wall of the sensory canal is clearly visible in some specimens, and particularly in isolated dentary bones as M297 and M299 (Text-figs. 8a; 9a, b).

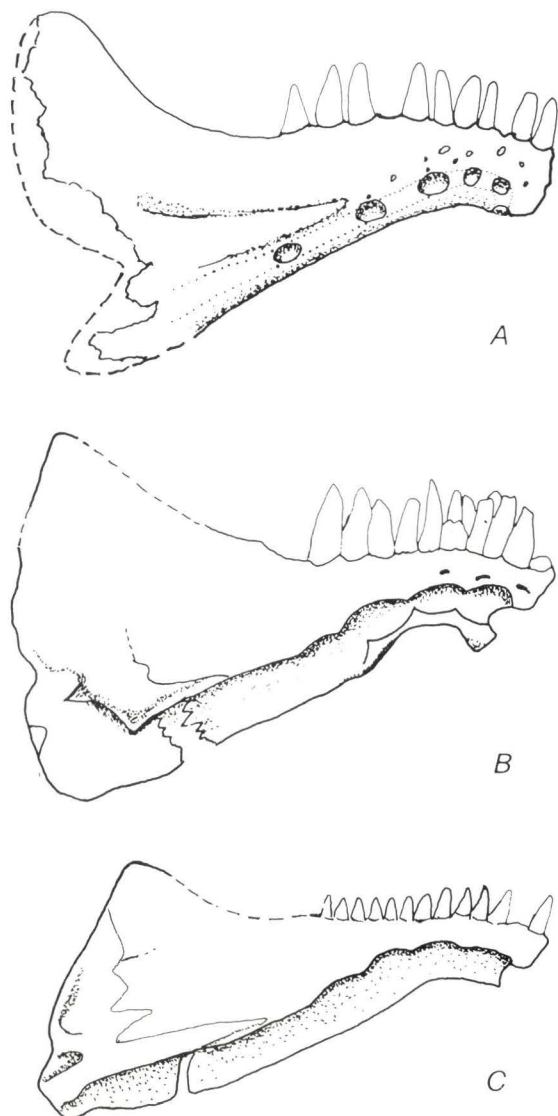
This condition is unusual in macrosemiids. Bartram (1977) found that in all the members of the family the mandibular sensory canal runs in an open trough.

In my opinion, it is possible that at least in some *Notagodus* (e.g.: specimens of *N. helenae* studied by Bartram), the thin lateral wall of the bony tube was crushed and not preserved, imitating an open trough.

The thin posterior margin of the dentary is developed as a sinuous suture as it overlaps the angulo-articular. The angulo-articular has a pock-marked surface in its hind corner, near the articulation with the quadrate.

PREOPERCULAR, HYOID ARCH AND OPERCULAR SERIES

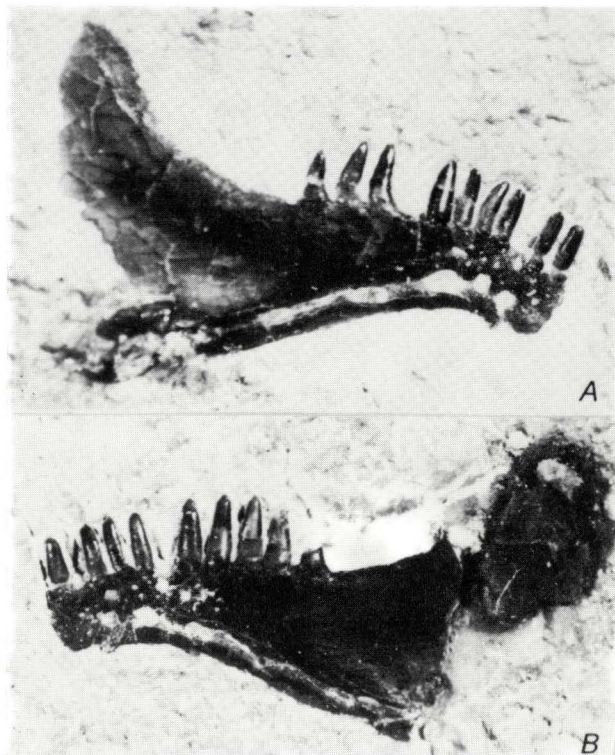
The preopercular is damaged in all the specimens. It is possible to observe a smoothly curved anterior border, while the posterior border is indented slightly opposite the interopercular. The horizontal limb of the preoperculum ends up near the quadrate-angular joint. The hyomandibular (M19271, M19297) is a massive bone with a subtriangular dorsal portion and a gently convex upper border. Ventrally, it forms a slender and antero-



Text-fig. 8 - Evolutive modifications in the mandibular sensory canal of the Macrosemiids: A) *Notagogus pentlandi* Agassiz, specimen M299; B) *Macrosemius rostratus* Agassiz; C) *Notagogus denticulatus* Agassiz. [B) and C) = specimens 37051 and P1090, B.M. (N.H.); from Bartram 1977, p. 145, fig. 4 and p. 192, fig. 38, partially redrawn and modified].

ventrally directed limb, the end of which remains obscured in the observed specimens.

The opercular series (Text-figs. 5, 6) is similar in shape and arrangement to that of *N. denticulatus* (compare Bartram 1977, p. 194, fig. 39; adult specimen). The opercular is almost twice as deep as broad. It bears ganoine ornament except along its anterior border. Also the subopercular and the interopercular are each ornamented by a few ganoine tubercles near the hind margins. The ceratohyal, par-



Text-fig. 9 - *Notagogus pentlandi* Agassiz. Isolated lower jaws (M299, M297). Lower Albian of Pietraroia. The mandibular sensory canal opening by pores is clearly visible. X 8.0 approx.

tially visible in the specimens, seems to be quite similar to that of *N. denticulatus*.

There are eight branchiostegal rays arranged as usual in *Macrosemius* and *Notagogus*; they are long and broaden distally.

VERTEBRAL COLUMN

Accounts or illustrations of the vertebral column in *N. pentlandi* have been given by Woodward (1895b: pl. 3, fig. 8) Bassani & D'Erasmo (1912: p. 208, fig. 2), Bartram (1977: p. 202). It can be useful to add something. The only specimen that shows the entire and well preserved vertebral column is M647, from Castellammare (Pl. 3, fig. B). It shows about 28 (30?) centra; each of which is composed by a ventral crescent bearing an haemal arch, a smaller dorsal crescent bearing a neural arch, and posteriorly, a dorsal intercalar crescent. In the last few caudal centra the three crescents are separate.

Proceeding anteriorly, at first the dorsal intercalar and the ventral crescent fuse among them, and finally the dorsal crescent, bearing the arch fuses, so that the anteriormost centra form a complete ring around the notochord.

Progressing anteriorly from the level of the anal origin, the dorsal crescents bearing the neural arches become progressively reduced in size, and the neural arches seem to lie directly on the dorsal ends of the ventral crescents that, correspondingly, increase in size.

The bone that constitutes the crescents is of a different kind from that of the arches: it is light-coloured and stratified; this difference is probably due to the notochordal origin of the crescents, whereas the arches are endochondral ossifications.

PECTORAL GIRDLE AND FIN

The post-temporal is triangular, ornamented with ganoine and bears a large sensory canal pore near the lower corner of the hind margin.

The cleithrum is gently curved and its hind border forms a shallow sinus opposite the fin insertion. Dorsally, the cleithrum curves forward beneath the posterior border of the opercular.

On the lateral surface near the anterior border of the cleithrum, there is at least one vertical row of very small denticles, as in *N. helenae*. It is not clear if a serrated appendage, homologous with that found by Bartram in *Propterus elongatus* Wagner 1863, is present (M19277, M19297).

The coracoid (M19271, text-fig. 10), poorly known in Macrosemiids, is a stout arch of bone as in *Propterus elongatus*.

The lower foot of the arch dilates in an antero-ventral, thin expansion, anteriorly ending with an acute angle and with a concave upper border and a convex and thickened postero-ventral border. This condition, with a completely ossified anterior process of the coracoid is unusual in Macrosemiids.

The pectoral fin contains at least 11-12 rays. The leading ray is strong and unbranched and bears the remains of fused fringing fulcra in its proximal part; distally, the fringing fulcra are more distinct, but also fused with the ray.

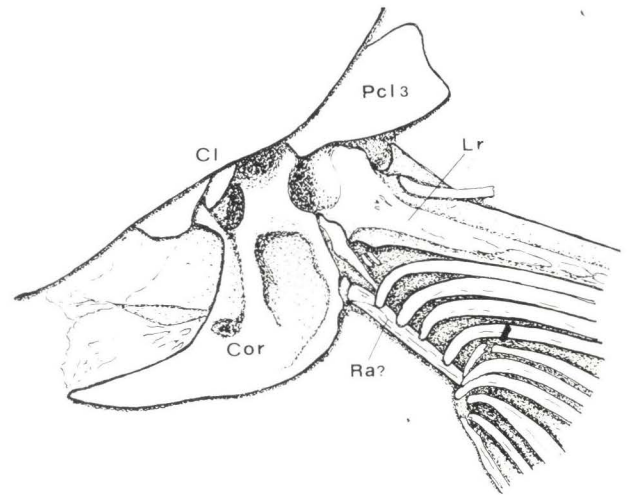
PELVIC GIRDLE AND FINS

The pelvic girdle was drawn by Bassani & D'Erasmus (1912).

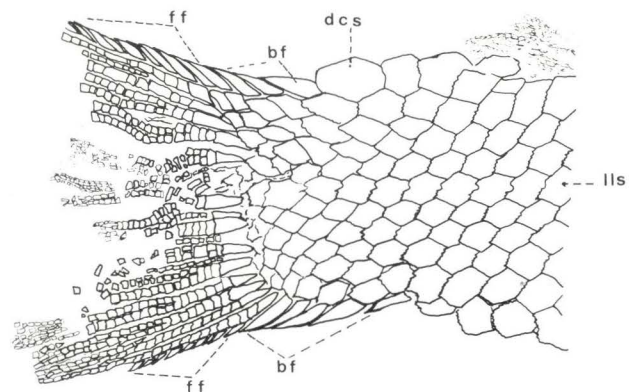
The ventral fin contains 6 rays; the first probably unbranched. Fringing fulcra are present.

DORSAL AND ANAL FINS

D1 is longer than D2 and contains 14-15 rays. The branched rays are preceded by at least one small, unbranched ray [B.M.N.H. P2065]; there are at least two small basal fulcra (M19270).



Text-fig. 10 - *Notagogus pentlandi* Agassiz. Part of pectoral girdle and fin in lateral view, as preserved in M19271. The coracoid shows the ossified anterior process.



Text-fig. 11 - *Notagogus pentlandi* Agassiz. Caudal portion of the trunk, as preserved in M19277.

The two lobes are separated by a very short gap. D2 contains 10-12 rays. The first is short, unbranched and unsegmented, the second, also unbranched, is longer than the first and distally segmented.

The anal fin contains at least 6-7 rays. Fringing fulcra are present.

CAUDAL SKELETON AND FIN

The caudal skeleton was partially described (the lower lobe) by Bassani & D'Erasmus (1912) and Bartram (1977). Between the six modified haemal elements that support the lower lobe rays, probably three are three hypurals (Text-fig. 12 and 13), because the groove near the articular head of the third element (Hpu1 in M647) probably signifies the exit point of the caudal artery and vein (Nybelin, 1963, p. 487).

The axial lobe contains at least two other small hypurals that articulate along the notochord which, in M647 (Text-fig. 12), seems to be enclosed by a single bone (fused uroneurals), but traces of suture or fusion between different, smaller pieces, are uncertain. In M645 (Text-fig. 13) these traces are visible, and the «urostyle» seems to be constituted by at least five or six ural-neural arches, the last of which articulates with the dorsal principal axial ray. It is not clear if the notochord was enclosed by these pieces or if it ran ventrally, in an open trough. Dorsally, there are remains of four, very oblong and slender bony elements preserved in M645: it is not clear if they were neural spines or epurals because they each lack proximal part. It is probable that, in contrast to *N. ferrerii* Wenz 1964 and *Enchelyolepis pectoralis* (Sauvage, 1883) (see Bartram, 1977, p. 167, fig. 21), the first two of them, are neural spines and only the last two are epurals. Distally, these elements articulate with the basal fulcra.

In the caudal fin, the usual condition I find in the adult specimens is: five rays in the axial lobe and eight in the lower one (the two external rays bears fringing fulcra and are unbranched).

Within the specimens from Castellammare, only two (M648, P2065) show six rays in the axial lobe. The young specimens, often show only four axial rays and six long rays in the lower lobe, preceded by two small external rays that, as Bartram hypothesized, lengthen in growth, constituting the eight usual lower rays. In the same young specimens, the lower lobe seems to be devoid of fringing fulcra, preceded only by few basal fulcra.

It is possible that the fringing fulcra develop in growth by the progressive shifting along the lower caudal margin, of the initial basal fulcra. In the

adults, the lower lobe is preceded by five basal fulcra.

SQUAMATION

N. pentlandi shows three postcleithral scales whose shape and position are shown in text-fig. 6.

There are 39 dorso-ventral rows of scales from the hind margin of the cleithrum to the basis of the upper caudal lobe.

The median dorsal scales, behind D2, are hexagonal, with a concave posterior border. This scale series ends with the «caudal scute», which is also hexagonal but larger and with a smooth and convex posterior margin. The caudal scute precedes the epaxial basal fulcra.

The arrangement and shape of the scales covering the flanks are shown in text-fig. 15.

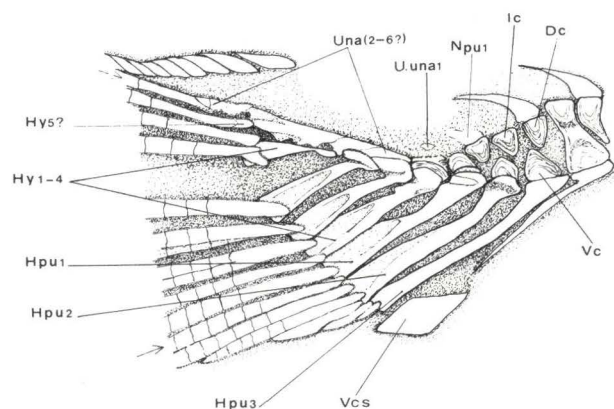
Behind the insertion of the ventral fin, there are rhomboidal scales, their height and width are nearly equal and their posterior border is indented in its upper part.

The origin of the anal fin is preceded by a large scale (Text-fig. 14a) which, in its exposed part, has an elliptical shape, with marginal and concentric ganoine ridges.

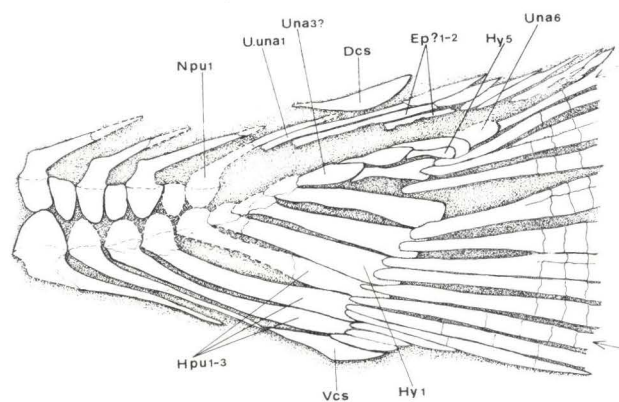
In front of this scale, there are several large scales of subquadrangular shape, the last of which has a pock-marked surface.

Along the ventral line, behind the anal fin, there are rhomboid equidiagonal scales with finely indented posterior borders forming an obtuse angle with each other.

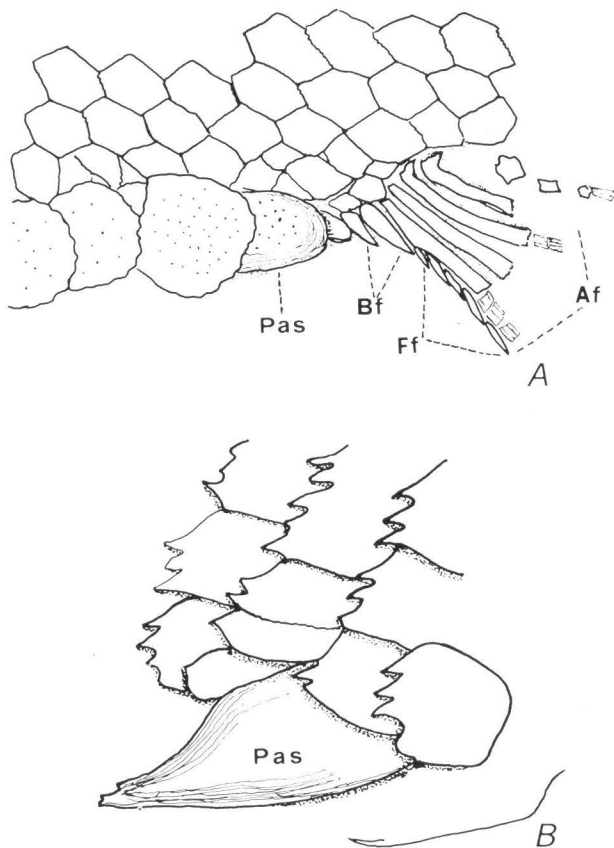
In young specimens (Museum of Naples), the scales are entirely cycloid; in the adult specimens cycloid scales are present only in narrow ventral



Text-fig. 12 - *Notagodus pentlandi* Agassiz. Caudal skeleton, as preserved in M647 (young specimen). The arrows indicate the first upper and lower full-length rays.



Text-fig. 13 - *Notagodus pentlandi* Agassiz. Caudal skeleton, as preserved in M645 (young specimen). The arrows indicate the first upper and lower full-length rays.



Text-fig. 14 - Preanal scale area in: A) *Notagodus pentlandi* Agassiz, as preserved in M19271; B) *Notagodus denticulatus* Agassiz, as preserved in P1090 B.M. (N.H.).

regions immediately behind the postcleithral scales, just above the origin of the pectoral fins.

There are 37-38 lateral line scales. The lateral line is marked by a small pore in a nearly central position on certain scales; the pore occurs with an irregular frequency on the scales, except beneath D2, where it appears on alternate scales.

The hind margin of each lateral line scale is marked by a small hollow (Text-fig. 11), larger than those due to the serration of the scales. The lateral line is complete. A dorsal, accessory lateral line is also present, it is marked by sporadic pores on the scales just below the dorsal fins.

COMPARISONS AND CONCLUSIONS

Notagodus pentlandi shows considerable similarities with *N. helenae*, from the lower Kimmeridgian of Cerin, Ain, France, and with *N. denticulatus* from the lower Tithonian of Kelheim and Eichstadt, in Bavaria.

N. helenae and *N. pentlandi* are similar in the body proportions. It can be useful to point out that Bartram (1977, p. 196) indicates a mean predorsal length (as percentage of standard length) of 33% in *N. helenae*. This is probably a misprint, because the predorsal length I got from the plate XX, figs. B, C, in De Saint-Seine (1949) is 42-43%, and it is close to that of *N. pentlandi* (44%).

N. helenae and *N. pentlandi* also have very similar supraorbitals, these being arranged in two rows in both species. In my opinion, it is possible that two rows of supraorbitals may be the usual condition in other species of the genus, in which the supraorbitals are generally unknown, because of their easy detachment after the death. According to the description of *N. helenae* given by Bartram, this species differs from *N. pentlandi* mainly in the following features: 1) the fringing fulcra are absent in the pectoral fins of *N. helenae*; in *N. pentlandi* they are present, but fused with the leading ray of the fin. 2) The pelvic fins do not bear fringing fulcra and there are five rays in *N. helenae*; fringing fulcra are present on the pelvic fin of *N. pentlandi* and there are six rays. 3) The anal fin differs in the number of rays (five in *N. helenae* and six or seven in *N. pentlandi*). 4) The hind border of each flank scale is entirely serrated in *N. helenae*; in *N. pentlandi* it is serrated only in its lower half. 5) *N. helenae* shows four postcleithral scales; they are three in *N. pentlandi*.

Differences are probably present also in the shape of the cleithrum. That in *N. helenae* shows a posterior expansion that De Saint-Seine (1949, p. 195, fig. 85) mistook for an anterior postcleithral scale. De Saint-Seine also described the mandibular sensory canal running in a bony tube in *N. helenae*, and opening by pores; Bartram (1977, p. 198) states that «the region of the mandible enclosing the sensory canal is not preserved in the specimens», but the description given by De Saint-Seine and their fig. 85, p. 195 convinced me that the situation in *N. helenae* is the same as I find in *N. pentlandi*.

Between *N. pentlandi* and *N. denticulatus*, the main differences I find are the following: 1) The condition of the mandibular sensory canal (see below). 2) In *N. denticulatus* all dorsal fin-rays are segmented and branched; in *N. pentlandi* the first ray of D1 and the first two rays of D2 are unbranched and the first ray of D2 is also unsegmented, moreover D1 bears few fringing fulcra in *N. denticulatus*, whereas they seem to be absent in *N. pentlandi*. 3) The predorsal length (as percentage of standard length) is 41% in *N. denticulatus* and 44% in *N. pentlandi*. 4) There are about 34 lateral line scales in *N. denticulatus*; in *N. pentlandi* they are 37-38. 5) There are four postcleithral scales in *N. denticulatus* and three in *N. pen-*

tlandi. 6) The preanal scales have different shape in the two species (see text-fig. 14).

Other differences are probably present in the shape of the quadratojugal, in the outline of the suture between the dentary and the angular (it is a zigzag suture in *N. denticulatus*), in the number of the anal fin-rays (at least four in *N. denticulatus*, six or seven in *N. pentlandi*), in the serration of the hind border of the scales, that seems to be more marked in *N. denticulatus*.

An important feature that differentiates *N. pentlandi* from all the other species ascribed to this genus and also from the other members of the family Macrosemiidae (see Bartram, 1977, p. 223, «specialization» 17), is the mandibular sensory canal that runs in a bony tube, opening by large pores in the anterior portion of the dentary; this is a primitive feature of which the other members of the family preserve a remnant expressed as the wavy outline of the upper and lower borders of the mandibular sensory canal (Text-fig. 8). This wavy edge makes it possible to recognize the position of the primitive pores (probably present during the early ontogenetic stages).

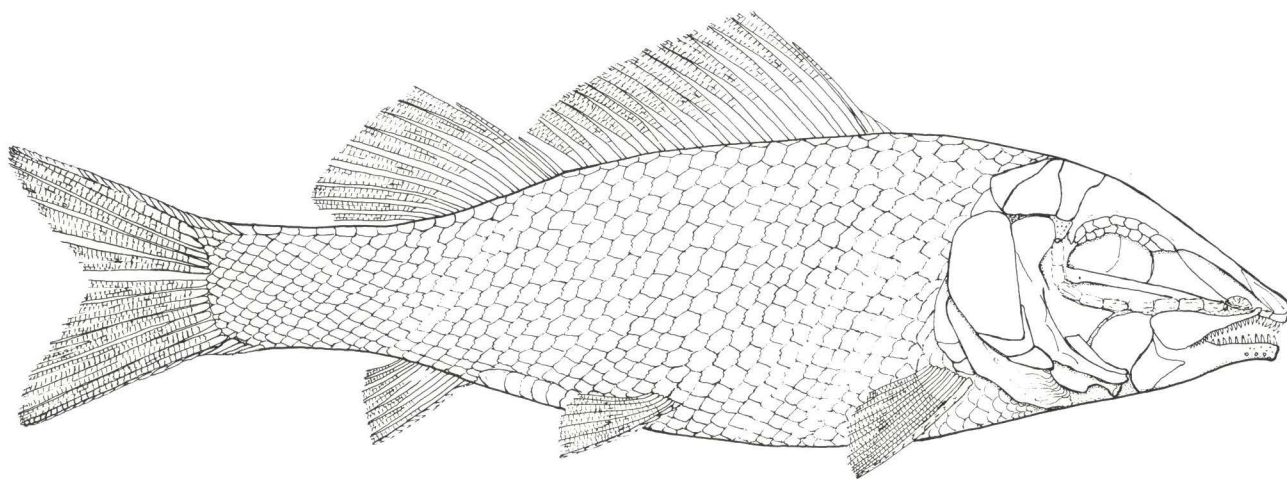
Also primitive for the family is the complete ossification of the coracoid in *N. pentlandi* (Text-fig. 10); this condition is unknown in the Macrosemiidae. Bartram (1977) stated that only the mesocoracoid arch was ossified in *Propterus elongatus* (and probably in *Macrosemius rostratus*), but the anterior process of the coracoid could be cartilaginous as in *Lepisosteus* (see also Patterson, 1973).

Also Olsen & McCune (1991) listed the reduction of ossification in the endochondral component of the shoulder girdle to only the mesocoracoid arch as a synapomorphy of the Semionotiformes (restricted to the Semionotidae, Macrosemiidae and Lepisosteidae).

The above described features suggest that *Notagodus* approaches primitive Macrosemiid condition, implying some modifications in the definition of the family to include forms with an enclosed mandibular sensory canal and a completely ossified coracoid. The definition of the genus *Notagodus* might be also revised, including in it only the forms that, as the type species, show the above mentioned primitive features together with some others, such as the double row of supraorbitals [at present they are *N. pentlandi* and, very probably *N. helenae* (the coracoid is unknown in the species)]. Accepting this, the emended diagnosis of the genus will be the following:

Genus NOTAGOGUS Agassiz 1835, emend.

Small, fusiform macrosemiid fishes; skull-roof bones covered with a layer of ganoine; sensory canals on skull of small diameter and completely enclosed in bone; frontoparietal suture slightly sinuous; dermopterotic very large, housing the lateral part of the supratemporal commissure; supratemporal absent; polygonal supraorbitals forming two rows; dermosphenotic incorporated into skull-roof; maxillary expansion asymmetrical, deep with straight oral border and convex upper and hind edges, maxillary teeth small, stout, forming a long row; dentary moderately curved, bearing stout teeth and with a sensory canal enclosed in the bone, opening by pores; anterior border of preopercular forming a regular curve, ventral limb not greatly deepened, surface of opercular covered by ganoine; completely ossified coracoid; pectoral fin with about 15 rays, fringing fulcra present but fused with the leading ray; pelvic fin with about six rays, fringing fulcra sometimes present; anal fin with about seven rays, basal and fringing fulcra present; dorsal fin



Text-fig. 15 - *Notagodus pentlandi* Agassiz. Restoration of skeleton.

divided into two closely spaced lobes, D1 with about 15 rays, D2 of about 10-12 rays, few basal fulcra are present; caudal fin with five or six axial lobe rays, weakly forked; squamation complete, forming a pattern of deepened hexagons, hind border of each scale pectinated at least in its lower half, ventral scales becoming cycloid; vertebral centra forming from dorsal and ventral crescents which can fuse into complete cylinders in the anterior part of the trunk.

Type species – *Notagodus pentlandi* Agassiz 1835.

Included species – *N. helenae*, *N. inimontis*?

On the other side, *N. denticulatus* can be indicated as the type species of a new genus, *Neonotagodus*, including less primitive forms, with the following diagnosis:

Genus NEONOTAGODUS n. gen.

Diagnosis – The same for *Notagodus sensu* Bartram 1977, but including: «supraorbitals arranged in a single row; mandibular sensory canal running in an open trough».

Type species – *Notagodus denticulatus* Agassiz 1839.

Included species – At present it is impossible to include with certainty other species in the genus, because of the state of preservation of the specimens and, consequently, the incompleteness of the data available in literature.

After this, a better knowledge of poorly known species as *N. decoratus* Eastman, *N. parvus* Traquair, *N. ferrerii* Wenz, is desirable to give them a correct taxonomic placing.

STRATIGRAPHICAL DISTRIBUTION AND ECOLOGY

Notagodus pentlandi Agassiz, the type species of the genus, represents, together with *Propterus scacchi* (Costa), one of the «younger» members of the Macrosemiidae. It is recorded only from the Upper Barremian of Castellammare and from the Lower Albian of Pietraroia (Southern Italy).

The oldest Macrosemiidae are from the Upper Trias whereas all the other species are from European late Jurassic deposits, except for *N. parvus* Traquair from the Neocomian of Bernissart (Belgium), and *N. ferrerii* Wenz and *Propterus vidali* Sauvage from the Spanish Neocomian (Montsech, Las Hoyas).

With regard to the ecology of these fishes, a number of late Jurassic and early Cretaceous Macrosemiids are found in association with reefs.

This seems true for the genera *Macrosemius*, *Propterus*, *Notagodus sensu* Bartram, 1977) and *Histionotus* in the lithographic limestones of Bavaria and Cerin (France). Therefore, they do appear to be linked with low-energy lagoon environments, sheltered by reefs from the open sea and probably in communication with rivers (Montsech and Las Hoyas, Spain) (De Saint-Seine, 1949; Barthel, 1970).

With regard to diet, Bartram (1977) suggests that these fishes, with their small mouths, reduced dentition, broad fins, etc. must have fed on plants and small benthos like crustaceans and molluscs. And they probably did this by moving slowly but skilfully between the reef.

Finally, it should be noted that De Saint-Seine (1949) records two specimens of *Notagodus* as prey of other fishes: a specimen of *Ionoscopus desori* with a *Notagodus* in its abdomen, and a specimen of *Belonostomus tenuirostris* with a *Notagodus* in its jaws; those two genera, *Ionoscopus* and *Belonostomus*, are also present in the limestones of Pietraroia.

ACKNOWLEDGEMENTS

I wish to thank Prof. P. De Castro (Department of Palaeontology, Naples) for his useful advice and Dr. C. Patterson (N.H.M. London), for the hospitality and help during my stay at The Natural History Museum and for the review and the observations made in the first draft of the manuscript and Dr. L. Sorbini (Mus. Civ. St. Nat., Verona), for the critical review. I also thank Prof. F. Barattolo (Dept. of Paleont., Naples) for the discussions about the statistics, Dr. M. Del Re (Conservator at the Museum of Palaeont., Naples) for her kindness in showing me the specimens and Dr. M. Parente and Dr. A. Gesuè for the second reading of the English version of the paper.

APPENDIX

ABBREVIATIONS USED IN THE FIGURES

Af	- Anal fin.
Ang	- Anguloarticular.
Ant	- Antorbital.
BD	- Body depth.
Bf	- Basal fulcra.
Br	- Branchiostegal ray(s).
Ch	- Ceratohyal.
Cl	- Cleithrum.
Cor	- Coracoid.
D	- Dentary.
Dc	- Dorsal crescent.
Dcs	- Dorsal caudal scute.
DI	- Left dentary.
Dpt	- Dermopterotic.
Dsp	- Dermosphentic.
Ep	- Epiural(s).

F	- Frontal.
Ff	- Fringing fulcra.
HL	- Head length.
Hm	- Hyomandibular.
Hpu	- Haemal pre-ural spine(s).
Hy	- Hypural(s).
Ic	- Intercalar crescent.
Io	- Infraorbital.
Iop	- Interopercular.
Lls	- Lateral line scale(s).
Lr	- Leading fin-ray.
Mpt	- Metapterygoid.
Mx	- Maxilla.
Npu	- Neural pre-ural arch(es).
Op	- Opercular.
Ors	- Orbitosphenoid.
P.	- Parietal.
PaL	- Preanal length.
Pas	- Preanal scale.
Pcl	- Postcleithral scale(s).
PdL	- Predorsal length.
Pmx	- Premaxilla.
Pop	- Preopercular.
PpL	- Prepelvic length.
Psph	- Parasphenoid.
Pt	- Post-temporal.
Q	- Quadrate.
Qj	- Quadratojugal.
Ra	- Radial.
Sc	- Sensory canal.
SL	- Standard length.
So	- Supraorbital(s).
Sop	- Subopercular.
Una	- Ural neural arch(es).
U.una	- Unmodified ural neural arch.
Vc	- Ventral crescent.
Vcs	- Ventral caudal scute.

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(manuscript received October 1, 1992
accepted December 23, 1993)

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